

The University of Chicago

EFFECT OF ALTERNATE
MOISTENING AND DRYING ON
GERMINATION OF SEEDS OF
WESTERN RANGE PLANTS

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF DOCTOR
OF PHILOSOPHY

DEPARTMENT OF BOTANY

1932

By
SYLVIA MAY GRISWOLD

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CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 475¹

SYLVIA M. GRISWOLD

(WITH NINE FIGURES)

Introduction

Although considerable study has been given to the germination behavior of various seeds, little is known regarding the effect that alternation of moistening and drying has upon their germination. In times of drought the seeds dry out and lie in that condition for an indefinite period. In preliminary tests conducted with the seeds of a large number of range plants from the Wasatch Plateau in central Utah, some of the seeds gave high percentages of germination under ordinary germinating conditions with continuous moisture at room temperature; others gave little or no germination under such conditions.

REVIEW OF LITERATURE

The literature includes few references concerning the seeds of range plants or the effect of drying after the seeds have absorbed water. SAMPSON (29, 30, 31, 32) reports the percentage of viability in germination tests of the seeds of a number of range plants² from

¹ In cooperation with the Intermountain Forest and Range Experiment Station of the United States Department of Agriculture, Forest Service.

² Owing to changes in nomenclature or in the check identification of certain species from the Manti National Forest by the Bureau of Plant Industry, ten of the species studied by SAMPSON are discussed in this report under other names:

Agropyron pauciflorum (Schwein.) Hitchc. (*A. tenerum* Vasey) not *A. violaceum* (Hornem.) Lange

Bromus anomalus Rupr. (*B. porteri* [Coult.] Nash.)

Bromus polyanthus Scribn. (*B. marginatus* Nees)

Melica bulbosa Geyer (*M. bella* Piper)

Poa secunda Presl. (*P. sandbergii* Vasey)

Stipa columbiana Macoun (*S. minor* Scribn.)

[Footnote continued on p. 244]

the Manti National Forest in central Utah, and the Wallowa National Forest in northeastern Oregon. Fourteen of the species which he studied (seven of which were from the Manti National Forest) are included in this investigation. In the tests conducted by SAMPSON most of the seeds gave low percentages of germination, but unless the conditions requisite for germination of each particular species are supplied, the results do not show the true viability of the seeds. The lack of adequate data regarding the conditions used in SAMPSON'S tests makes a comparison of results impossible.

Several investigators have studied the effect of reduced moisture content on germination, using fresh seeds for desiccation. EWART (10) concluded that the moisture content could not be reduced below 2 or 3 per cent without seriously affecting the vitality of the seeds. Others (9, 14, 25, 28, 33, 35) found that the water content could be reduced below this point, in some instances to a mere trace of moisture, with little or no effect on subsequent germination. ATTERBERG (1) observed that drying immature barley seeds at 37° C. increased the percentage of germination over seeds dried at lower temperatures, but drying soaked seeds of high germinative capacity at 48° to 50° C. or higher, reduced the percentage of germination.

From experiments with *Brassica alba*, KIDD (20) and KIDD and WEST (21) discovered that drying seeds during an early stage of development previous to germination accelerated germination when the seeds were remoistened, but drying the seeds after cell division had advanced resulted in injury. They found also that secondary dormancy was broken by complete redrying, or by removal of the seed coat, followed by remoistening. They interpret such germination as the result of mechanical stimulus on the embryo and not as changes within the seed coat, although removing the coats gave 100 per cent germination within a day after moisture was supplied. The effect of desiccation on the seed coats of certain water plants (4, 23) has long been known to be beneficial to germination.

The seed coat, according to CROCKER (3, 4, 5, 6), is most frequent-

Artemisia incompta Nutt. not *A. discolor* Dougl.

Lepidium densiflorum Schrad. (*L. ramosissimum* A. Nels.)

Pentstemon rydbergii A. Nels. not *P. procerus* Dougl.

Pseudocymopterus montanus (A. Gray) Coult. and Rose (*P. tidestromii* Coult. and Rose).

ly the cause of delayed germination. It may prevent the absorption of water (11, 13, 15, 16, 26) or oxygen (2, 3, 34), or may mechanically restrain the embryo from developing (6, 7). The seeds of *Amaranthus retroflexus* (6), *Avena fatua* (2, 36), and some of the grains (1, 22) have been found to germinate better after a period of dry storage. CROCKER interprets the changes in *Amaranthus retroflexus* as due to hysteretic changes in the colloids of the seed coat, which lower the elasticity and the breaking strength of the coat (6). Changes in other seeds might harden the seed coat or affect the permeability to oxygen or water, as observed by DUVEL (9). Not only the seeds of different species, but the seeds of a given species may also vary in their oxygen requirement (3, 34). CROCKER (3) found that the rate of diffusion of oxygen through the seed coat of *Xanthium* was increased when the coat was allowed to become somewhat dry.

MUNERATI and ZAPPAROLI (24) investigated the effect of alternately moistening and drying the seeds of several noxious weeds. For 17 months they subjected the seeds to short (15 days) and long (3 months) periods of drying following a 15-day period of moistening. In four species germination was increased materially by both short and long periods of drying, while with two species there was only a slight increase. Drying decreased the germination of one species and had no effect upon another.

PURPOSE OF INVESTIGATION

The purpose of this investigation was to seek information concerning the following questions: What effect would an alternation of moistening and drying for short periods have upon the seeds of the different species of range plants? Would it hasten or delay the germination of seeds exposed to such conditions? Would it affect the percentage of germination? Might it have a beneficial effect upon the germination of seeds which gave little or no germination with continuous moisture at room temperature, or would the seeds be injured? Would seeds dried after being in moist conditions for some time without germinating, still retain their viability; that is, would seeds in which the processes of after-ripening and embryo development were interrupted by drying, germinate when again supplied with moisture?

Materials and methods

SPECIES STUDIED

Many of the "seeds" studied are fruits rather than seeds, but for the sake of convenience, the terms seed and seed coat are used regardless of the origin of the enveloping structures. Seeds of the following 42 species³ were chosen to study the effect of alternate moistening and drying for short periods. For the long period of drying only 25 of the 42 species were used.

GRASSES.—*Agropyron pauciflorum* (Schwein.) Hitchc. (*A. tenerum* Vasey), *Bromus anomalus* Rupr. (*B. porteri* [Coul.] Nash), *B. polyanthus* Scribn., *Hordeum nodosum* L., *Melica bulbosa* Geyer, *Poa interior* Rydb., *P. secunda* Presl. (*P. sandbergii* Vasey), *Stipa columbiana* Macoun, and *S. lettermani* Vasey.

HERBS OTHER THAN GRASSES.—*Achillea lanulosa* Nutt., *Androsace diffusa* Small., *Artemisia incompta* Nutt., *Castilleja sulphurea* Rydb., *Chenopodium album* L., *Collomia linearis* Nutt., *Delphinium barbeyi* Huth., *Erythronium parviflorum* (S. Wats.) Goodding, *Frasera speciosa* Dougl., *Geranium viscosissimum* Fisch. & Mey., *Gilia pulchella* Dougl., *Lepidium densiflorum* Schrad., *Lupinus parviflorus* Nutt., *Moldavica parviflora* (Nutt.) Britton, *Orthocarpus tolmiei* Hook & Arn., *Pentstemon rydbergii* A. Nels., *P. subglaber* Rydb., *Plantago tweedyi* A. Gray, *Polemonium foliosissimum* A. Gray, *Polygonum douglasii* Greene, *Pseudocymopterus montanus* (A. Gray) Coul. & Rose, *Rudbeckia occidentalis* Nutt., *Rumex mexicanus* Meisn., *Sophia hartwegiana* (Fourn.) Greene, *Vicia americana* Muhl., and *Viola linguaefolia* Nutt.

WOODY SPECIES.—*Acer grandidentatum* Nutt., *Cercocarpus montanus* Raf., *Chrysothamnus lanceolatus* Nutt., *Ribes inebrians* Lindl., *R. montigenum* McClatchie, *Sambucus microbotrys* Rydb., and *Symphoricarpos oreophilus* A. Gray.

The form of *Agropyron pauciflorum* studied is the wheatgrass heretofore incorrectly known as *A. violaceum*. *Bromus polyanthus* is considered by HITCHCOCK (17) to be only a form of *B. carinatus*, but

³ Identification of all species has been checked with specimens in the herbarium of the Great Basin Branch Station, which have been identified by the Bureau of Plant Industry; or when there has been any question of doubt, the plants themselves have been checked by the Bureau of Plant Industry.

in accordance with the older usage, it is here treated as a species. *Achillea lanulosa* includes the subspecies *A. lanulosa alpicola* Rydb.

COLLECTION AND STORAGE

The seeds were collected from plants in their natural habitat after they had ripened but prior to dissemination, except a few seeds of *Collomia*, *Polygonum*, and *Viola* which were taken from the ground soon after dissemination. The collections were made between August 16 and September 17, 1928, in the region of the Great Basin Branch of the Intermountain Forest and Range Experiment Station on the Manti National Forest in central Utah. The seeds of each species were collected from definite areas. In the case of *Poa secunda*, collections were made from two areas. These were kept separate and are designated as *P. secunda* no. 1 and *P. secunda* no. 2. The seeds from dry fruits were placed directly in paper containers. Those from fleshy fruits were washed free from pulp and air-dried before they were placed in paper containers. All seeds were later placed in bottles with cork stoppers and stored at room temperature.

GERMINATION TESTS

The germination tests were made in the laboratories of the University of Chicago during a period extending from December 1928 to February 1930.

In preparation for these tests the seeds were disinfected in a 0.25 per cent solution of uspulun for 30 minutes and then rinsed in sterile water twice for 15 minutes each. They were then placed on sterile, moist cellucotton in petri dishes. Usually 50 seeds of a given species were used in each test, but for *Erythronium*, *Frasera*, *Geranium*, *Lupinus*, *Polygonum*, *Vicia*, *Acer*, and *Cercocarpus* 20 or 25 seeds were often used. As soon as the seeds germinated the seedlings were counted and discarded. Seeds were considered to have germinated when the hypocotyl protruded through the seed coat to an extent of 5 mm. or more.

To study the effect of short periods of alternate moistening and drying on the germination of the seeds included in this investigation, three sets of seeds were used, all of which were kept at room temperature. During the period of the experiment the temperature of the

room varied between 22° and 29° C. The temperatures used for drying are considerably lower than those used by ATTERBERG in his experiments with barley.

In one set of seeds (*A*), the substrate was kept moist continuously during the period of the test. In the second set (*B*) the substrate was kept moist for 5-7 days, then allowed to dry out by opening the petri dishes to permit evaporation. The dishes were left open until the cellucotton appeared thoroughly dry, then the substrate was remoistened and the dishes closed for three days, after which they were opened and the contents again allowed to dry. This process of alternate moistening and drying was repeated until the test had run for 51 to 53 days. Each period of drying required two or three days, depending upon the humidity of the atmosphere at the time. As an aid in preventing mold and bacterial growth, the petri dishes were kept in a case with cloth-covered sides which permitted the circulation of air but kept out dust and other foreign material.

The third set of seeds (*C*) was also subjected to alternate moistening and drying, but the period of moistening preceding the period of drying was shorter than that used in test *B*. Drying also took place more slowly. This set of seeds was not placed in conditions for germination until after the close of test *B*. The seeds were prepared as for *A* and *B* and placed on moist cellucotton for one day, after which the petri dishes were opened to dry. A period of high humidity prevailed at the time; consequently evaporation took place slowly and 12 days were required to dry out the substrate and seeds. They were then remoistened for one day and again allowed to dry out, which required four days. After a further period of three days under moist conditions the test was discontinued.

At the end of the period of alternate moistening and drying in both tests *A* and *B*, many of the seeds which had not germinated still looked healthy. With the exception of two species, *Lepidium* and *Rumex*, the seeds which had not germinated in test *B* were placed immediately in other conditions for germination to determine whether they had retained their viability. The seeds of *Lepidium* and *Rumex* were left in alternating moisture conditions for an additional 20 days. The seeds of the remaining species from test *B* were

remoistened, placed at 0° to 3° C. for eight days, then changed to room temperature of 22° to 29° C. for 12 days. At the end of the 12-day period the seeds of all but the following ten species were discarded. The seeds of *Delphinium*, *Pentstemon subglaber*, and *Ribes inebrians* were dried and kept for a later test. The seeds of seven species, *Collomia*, *Erythronium*, *Frasera*, *Gilia*, *Orthocarpus*, *Polemonium*, and *Polygonum*, were left for a further period of 120 days in a Minnesota germinator at 22° to 29° C. Following this long period at warm temperatures *Collomia* and *Frasera* were placed directly at alternating temperatures. The seeds of the other five species, *Erythronium*, *Gilia*, *Orthocarpus*, *Polemonium*, and *Polygonum*, were placed at cold temperatures of 0° to 3° C. for 34 days, then placed at alternating temperatures.

From test C the seeds of only five species were kept for further study. *Agropyron*, *Hordeum*, *Rumex*, *Viola*, and *Symphoricarpos* seeds were dried for 105 days to be used with other seeds in the following test.

To determine the effect of a long period of drying upon seeds which had been in moist conditions for some time, seeds which had failed to germinate under various conditions extending from 21 to 204 days were air-dried and kept at room temperature in paper containers for 105 days. Forty-eight samples representing 25 species were used. Three of the 48 samples were from the set of seeds subjected to alternating moisture conditions for 51 to 53 days (test B) and five samples were from those seeds which had been subjected to alternating moisture conditions for 21 days (test C), as previously noted. The remaining 40 samples were taken from seven other germination tests in all of which the seeds were kept moist continuously, but in which different temperature conditions had been used.

After drying for 105 days, the seeds were disinfected as for other tests and placed in petri dishes on sterile moist cellucotton. The seed coats of one set of *Vicia* seeds were broken by filing before they were placed in moist conditions. The seeds of each species were then placed under temperature conditions which were known or considered to be favorable for germination. The following were the temperature conditions used:

TABLE I
EFFECT OF ALTERNATE MOISTENING AND DRYING OF
SEEDS ON GERMINATION

SPECIES	PERCENTAGE GERMINATION			
	WITH CON- TINUOUS MOISTURE	UNDER ALTERNATING MOISTURE CONDITIONS		MAXIMUM GERMINATION OBTAINED IN OTHER TESTS
		RAPID DRYING	SLOW DRYING	
Grasses				
Agropyron pauciflorum.....	6	2	4	86
Bromus anomalus.....	94	80	94	100
B. polyanthus.....	98	100	98	100
Hordeum nodosum.....	0	0	0	100
Melica bulbosa.....	0	0	0	94
Poa interior.....	96	98	80	100
P. secunda no. 1.....	64	68	40	86
P. secunda no. 2.....	16	20	2	58
Stipa columbiana.....	38	34	32	84
S. lettermani.....	10	26	16	98
Herbs other than grasses				
Achillea lanulosa.....	82	98	36	100
Androsace diffusa.....	52	62	10	38
Artemisia incompa.....	58		76	86
Castilleja sulphurea.....	0	0	2	10
Chenopodium album.....	12	10	2	22
Collomia linearis.....	0	0	0	62
Delphinium barbeyi.....	0	0	0	2
Erythronium parviflorum.....	0	0	0	70
Fraseria speciosa.....	0	0	0	45
Geranium viscosissimum.....	100	95	85	100
Gilia pulchella.....	0	0	0	32
Lepidium densiflorum.....	48	90	48	100
Lupinus parviflorus.....	95	70	75	100
Moldavica parviflora.....	2	2	0	4
Orthocarpus tolmiei.....	0	0	0	42
Pentstemon rydbergii.....	4	16	0	30
P. subglaber.....	0	2	0	22
Plantago tweedyi.....	80	84	98	100
Polemonium foliosissimum.....	0	0	0	30
Polygonum douglasii.....	0	0	0	5
Pseudocymopterus montanus.....	86	72	46	88
Rudbeckia occidentalis.....	60	44	90	98
Rumex mexicanus.....	22	52	0	100
Sophia hartwegiana.....	2	2	2	6
Vicia americana.....	0	5	5	100
Viola linguaefolia.....	0	0	0	2
Woody species				
Acer grandidentatum.....	0	0	0	53
Cercocarpus montanus.....	5	10	10	65

TABLE I—*Continued*

SPECIES	PERCENTAGE GERMINATION			
	WITH CON- TINUOUS MOISTURE	UNDER ALTERNATING MOISTURE CONDITIONS		MAXIMUM GERMINATION OBTAINED IN OTHER TESTS
		RAPID DRYING	SLOW DRYING	
	TEST A	TEST B	TEST C	
<i>Chrysothamnus lanceolatus</i>	86	64	48	80
<i>Ribes inebrians</i>	0	0	0	98
<i>R. montigenum</i>	0	0	0	17
<i>Sambucus microbotrys</i>	0	0	0	6
<i>Symphoricarpos oreophilus</i>	0	0	0	32

1. Cold, 0° to 3° C. for the period of the test.

2. Alternating temperatures, 0° to 3° C. and 17° to 22° C. for approximately 12 hours each during the period of the test.

3. Cold, 0° to 3° C. for 8 days, then 22° to 27° C. until the end of the test.

4. Cold, as preceding for 8 days, then alternating temperatures as above until the end of the test.

The seeds were left in these conditions for 76 to 91 days.

Results

Tables I to IV give the results of the tests on the effect of short periods of alternate moistening and drying on the germination of the seeds included in this investigation. Table I gives for each species the various percentages of germination. The last column gives the maximum percentage of germination obtained in various other tests made from the same lots of seeds during a period extending from December 1928 to February 1932. The complete results of these tests will be published in a subsequent paper. While the results in the last column do not give a true index of viability for all of the species studied, they do provide a basis for comparison with the results obtained from the seeds under conditions of alternating moisture.

The seeds of the following 16 species gave no germination at room

temperatures, either with continuous moisture or with alternate moistening and drying. *Acer grandidentatum*, *Collomia linearis*, *Delphinium barbeyi*, *Erythronium parviflorum*, *Frasera speciosa*, *Gilia*

TABLE II
COMPARISON OF PERCENTAGE AND TIME OF GERMINATION OF
SEEDS UNDER THREE CONDITIONS OF MOISTURE

SPECIES	GERMINATION					
	CONTINUOUS MOISTURE		ALTERNATING MOISTURE CONDITIONS			
			RAPID DRYING		SLOW DRYING	
	DAYS REQUIRED	PERCENT- AGE	DAYS REQUIRED	PERCENT- AGE	DAYS REQUIRED	PERCENT- AGE
Grasses						
Bromus anomalus.....	5-25	94	3-34	80	4-14	94
B. polyanthus.....	3-16	98	3-25	100	4-12	98
Poa interior.....	3-13	96	3- 8	98	4-21	80
P. secunda no. 1.....	3-37	64	3-16	68	4-10	40
P. secunda no. 2.....	5-30	16	5-16	20	14	2
Stipa columbiana.....	3-39	38	3-25	34	4-12	32
S. lettermani.....	22-37	10	11-34	26	7-18	16
Herbs other than grasses						
Achillea.....	2-52	82	4-28	98	7-21	36
Androsace.....	4-26	52	9-52	62	7	10
Artemisia.....	4-46	58			4-14	76
Chenopodium.....	2- 9	12	2-12	10	21	2
Geranium.....	3-18	100	5-20	95	4-21	85
Lepidium.....	3-51	48	3-53	90	4-21	48
Lupinus.....	5-53	95	10-48	70	4-21	75
Pentstemon rydbergii...	9-23	4	13-48	16		0
Plantago.....	3- 6	80	7-13	84	4-18	98
Pseudocymopterus.....	9-28	86	13-20	72	12-21	46
Rudbeckia.....	3- 9	60	7-10	44	4-13	90
Rumex.....	23-25	22	24-53	52		0
Woody species						
Chrysothamnus.....	6-49	86	10-44	64	4-21	48

pulchella, *Hordeum nodosum*, *Melica bulbosa*, *Orthocarpus tolmiei*, *Polemonium foliosissimum*, *Polygonum douglasii*, *Ribes inebrians*, *R. montigenum*, *Sambucus microbotrys*, *Symphoricarpos oreophilus*, *Viola linguaefolia*.

The following seven species gave from 2 to 10 per cent only: *Agropyron pauciflorum*, *Castilleja sulphurea*, *Cercocarpus montanus*,

Moldavica parviflora, *Pentstemon subglaber*, *Sophia hartwegiana*, *Vicia americana*.

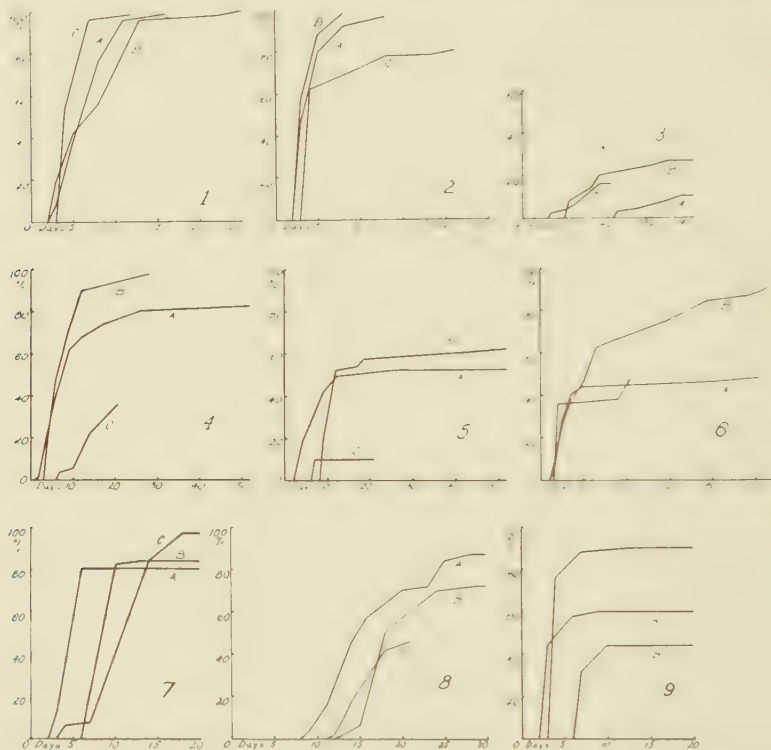
The time required for the germination of the seeds in tests *A*, *B*, and *C*, with the percentage of germination obtained for each of the 19 species which gave over 10 per cent germination at room temperatures, is shown in table II.

TABLE III
EFFECT OF ALTERNATE MOISTENING AND DRYING
ON PERCENTAGE OF GERMINATION

SPECIES	PERCENTAGE GERMINATION			
	INCREASE WITH RAPID DRYING	INCREASE WITH SLOW DRYING	DECREASE WITH RAPID DRYING	DECREASE WITH SLOW DRYING
<i>Bromus anomalus</i>		2	14	
<i>B. polyanthus</i>	2	0		0
<i>Poa interior</i>	2			16
<i>P. secunda</i> no. 1.....	4			14
<i>P. secunda</i> no. 2.....	4			10
<i>Stipa columbiana</i>			4	4
<i>S. lettermani</i>	16	16		
<i>Achillea lanulosa</i>	16			38
<i>Androsace diffusa</i>	10			40
<i>Artemisia incompta</i>		26		
<i>Chenopodium album</i>			2	10
<i>Geranium viscosissimum</i>			5	15
<i>Lepidium densiflorum</i>	42	4		
<i>Lupinus parviflorus</i>		5	25	
<i>Pentstemon rydbergii</i>	12			2
<i>Plantago tweedyi</i>	4	18		
<i>Pseudocymopterus montanus</i>			14	24
<i>Rudbeckia occidentalis</i>		30	16	
<i>Rumex mexicanus</i>	30			22
<i>Chrysothamnus lanceolatus</i>			22	2

The influence of alternate moistening and drying as shown by increase or decrease in percentage of germination is given in table III. Since the test in which the seeds were dried slowly (*C*) extended over a period of 21 days only, and tests *A* and *B* extended over 51 to 53 days, the final results of test *C* are not comparable with the other two except in six species, *Poa interior*, *P. secunda* no. 2, *Chenopodium*, *Geranium*, *Plantago*, and *Rudbeckia*, in which germination occurred within 21 days. However, the effect of alternating moisture

conditions on the percentage and the rate of germination during the period of test C' and the early period of tests A and B may be compared. The increase or decrease in percentage of germination of the



FIGS. 1-9.—Graphs showing rate and percentage of seed germination: A, given continuous moisture; B, subjected to alternating moisture conditions in which drying was rapid; C, subjected to alternating moisture conditions with slow drying. Fig. 1, *Bromus polyanthus*; fig. 2, *Poa interior*; fig. 3, *Stipa lettermani*; fig. 4, *Achillea lanulosa*; fig. 5, *Androsace diffusa*; fig. 6, *Lepidium densiflorum*; fig. 7, *Plantago tweedyi*; fig. 8, *Pseudocymopterus montanus*; fig. 9, *Rudbeckia occidentalis*.

seeds from test C' is based, therefore, on the germination of seeds which were kept moist continuously (test A) for a period of 21 days, and not on the final percentage of germination. Decreased germination was accompanied by a delay and increased germination by hastening, except with *Poa secunda* no. 1, *Androsace*, *Plantago*, *Rudbeckia*, and *Rumex*, in which a delay at first was followed later

by increased germination. In *Rudbeckia* and *Rumex* the retardation was slight. Differences of 5 per cent or less in germination results are not considered of importance. Figures 1 to 9 show the percentage and rate of germination in each of nine species representative of the different ways in which the seeds were affected.

TABLE IV
GERMINATION OF SEEDS FROM TEST B AFTER PERIOD
OF ALTERNATE MOISTENING AND DRYING

SPECIES	PERCENTAGE GERMINATION		
	DURING PERIOD OF ALTERNATE MOISTENING AND DRYING	AFTER PERIOD OF ALTERNATE MOISTENING AND DRYING	TOTAL
Grasses			
Agropyron pauciflorum.....	2	20	22
Hordeum nodosum.....	0	74	74
Poa secunda no. 1.....	68	2	70
P. secunda no. 2.....	20	6	26
Herbs other than grasses			
Achillea lanulosa.....	98	2	100
Collomia linearis.....	0	62	62
Frasera speciosa.....	0	5	5
Gilia pulchella.....	0	8	8
Lepidium densiflorum.....	90	2	92
Lupinus parviflorus.....	70	5	75
Pentstemon rydbergii.....	16	6	22
P. subglaber.....	2	12	14
Plantago tweedyi.....	84	2	86
Polemonium foliosissimum.....	0	20	20
Polygonum douglasii.....	0	5	5
Rumex mexicanus.....	52	2	54
Vicia americana.....	5	30	35
Woody species			
Chrysothamnus lanceolatus.....	64	2	66
Ribes inebrians.....	0	2	2

GERMINATION OF SEEDS AFTER ALTERNATE
MOISTENING AND DRYING

Some of the seeds which failed to germinate when subjected to alternating moisture conditions with rapid drying (test B) germinated when placed in other conditions following the period of alternate moistening and drying (table IV).

TABLE V
GERMINATION OF SEEDS SUBJECTED TO LONG PERIOD OF DRYING

SPECIES	No. SEEDS USED	FIRST GERMINATING CONDITIONS	PER- CENT- AGE GERMI- NATION	No. SEEDS DRIED	GERMINATING CONDITIONS AFTER DRYING	PER- CENT- AGE DRIED SEEDS GERMI- NATING
Agropyron.....	50	Alternating moisture 21 days	4	48	Cold, then warm	41
Hordeum.....	50	23° to 25° 35 "	4	42	Alt. temp.	97
Hordeum.....	50	Alternating moisture 21 "	0	49	Alt. temp.	96
Melica.....	50	-1.5° to -2.5° 10 "	0	49	Cold	94
Melica.....	50	23° " 25° 25 "				
Melica.....	50	19° " 24° 35 "	0	49	Cold	84
Melica.....	50	22° " 29° 74 "	0	49	Cold	92
Androsace.....	50	3° " 7° 96 "	0	46	Alt. temp.	20
Castilleja.....	50	17° " 21° 51 "				
Castilleja.....	50	3° " 7° 96 "	2	45	Cold, then alt. temp.	4
Castilleja.....	50	17° " 21° 51 "				
Castilleja.....	50	22° " 29° 74 "	0	36	Cold, then alt. temp.	0
Chenopodium....	50	22° " 29° 74 "	12	41	Cold, then alt. temp.	2
Chenopodium....	50	19° " 24° 35 "	8	42	Cold, then alt. temp.	7
Chenopodium....	50	3° " 7° 96 "	18	41	Cold, then alt. temp.	0
Collomia.....	50	17° " 21° 51 "				
Collomia.....	50	22° " 29° 74 "	0	41	Cold, then alt. temp.	7
Collomia.....	50	3° " 7° 96 "	40	29	Cold, then alt. temp.	13
Delphinium.....	50	17° " 21° 51 "				
Delphinium.....	50	3° " 7° 96 "	2	48	Cold, then alt. temp.	0
Delphinium.....	50	17° " 21° 51 "				
Delphinium.....	50	Alternating moisture 53 "	0	27	Cold, then alt. temp.	0
Erythronium....	20	22° to 29° 74 "	0	19	Cold, then alt. temp.	0
Frasera.....	20	22° " 29° 74 "	0	16	Cold, then alt. temp.	25
Gilia.....	50	22° " 29° 74 "	0	23	Cold, then alt. temp.	9
Gilia.....	25	3° " 7° 96 "	0	24	Cold, then alt. temp.	12
Gilia.....	25	17° " 21° 51 "				
Lupinus.....	20	3° " 7° 96 "	90	2	Cold, then alt. temp.	50
Lupinus.....	20	17° " 21° 51 "				
Moldavica.....	50	22° " 29° 74 "	2	48	Alt. temp.	0
Moldavica.....	50	18° " 22° 204 "	2	48	Alt. temp.	0
Moldavica.....	50	3° " 7° 96 "	2	48	Cold, then alt. temp.	0
Orthocarpus....	50	17° " 21° 51 "				
Orthocarpus....	50	19° " 24° 35 "	0	49	Cold, then alt. temp.	0
Orthocarpus....	50	3° " 7° 96 "	4	46	Cold	0
Orthocarpus....	50	17° " 21° 51 "				

TABLE V—*Continued*

SPECIES	No. SEEDS USED	FIRST GERMINATING CONDITIONS		PER- CENT- AGE GERMI- NATION	No. SEEDS DRIED	GERMINATING CONDITIONS AFTER DRYING	PER- CENT- AGE DRIED SEEDS GERMI- NATING
<i>Pentstemon ryd- bergii</i>	50	3° to 17° "	7° 96 days 21° 51 "	14	43	Cold, then alt. temp.	19
<i>P. subglaber</i>	50	Alternating moisture	53 "	2	46	Cold, then alt. temp.	13
<i>P. subglaber</i>	50	3° to 17° "	7° 96 " 21° 51 "	6	47	Cold, then warm	0
<i>Polemonium</i>	50	22° "	29° 74 "	2	46	Cold, then alt. temp.	26
<i>Polemonium</i>	50	3° " 17° "	7° 96 " 21° 51 "	4	46	Cold, then warm	9
<i>Rumex</i>	50	Alternating moisture	21 "	0	50	Alt. temp.	86
<i>Sophia</i>	50	3° to 17° "	7° 96 " 21° 51 "	0	46	Cold, then warm	2
<i>Vicia</i>	25	3° " 17° "	7° 96 " 21° 51 "	8	22	Seed coat filed; cold then warm	100
<i>Vicia</i>	25	23° "	25° 26 "	0	16	Cold, then alt. temp.	0
<i>Viola</i>	50	Alternating moisture	21 "	0	37	Cold, then alt. temp.	0
<i>Ribes inebrians</i> ...	50	23° to 3° "	25° 35 " 7° 97 "	0	45	Alt. temp.	4
<i>Ribes inebrians</i> ...	25	3° " 17° "	7° 97 " 21° 51 "	0	24	Cold, then alt. temp.	17
<i>Ribes inebrians</i> ...	50	Alternating moisture	53 "	0	36	Cold, then alt. temp.	3
<i>Ribes inebrians</i> ...	50	22° to	29° 74 "	0	44	Cold, then alt. temp.	0
<i>R. montigenum</i> ...	50	23° " 3° "	25° 35 " 7° 97 "	0	33	Alt. temp.	0
<i>R. montigenum</i> ...	25	3° " 17° "	7° 97 " 21° 51 "	0	24	Cold, then alt. temp.	17
<i>Sambucus</i>	50	23° " 3° "	25° 35 " 7° 97 "	0	44	Alt. temp.	0
<i>Sambucus</i>	50	3° " 17° "	7° 97 " 21° 51 "	0	50	Cold, then warm	0
<i>Sambucus</i>	50	22° "	29° 74 "	0	48	Cold, then alt. temp.	0
<i>Symphoricarpos</i> ..	50	23° " 25° 35 "	25° 35 "	0	43	Alt. temp.	0
<i>Symphoricarpos</i> ..	50	Alternating moisture	21 "	0	42	Cold, then alt. temp.	0
<i>Symphoricarpos</i> ..	50	18° to	22° 204 days	0	32	Cold, then alt. temp.	3

Of the five species which were kept from test *C*, the *Agropyron* seeds gave 40 per cent, *Hordeum* 94 per cent, and *Rumex* 86 per cent additional germination. *Symphoricarpos* and *Viola* seeds did not germinate under the new conditions.

GERMINATION AFTER LONG PERIOD OF DRYING

Percentages of germination obtained with the seeds which had been dried for 105 days after having been in moist conditions for varying lengths of time are shown in table V. Nineteen of the 25 species and 28 of the 48 samples used gave varying percentages of germination.

Discussion

The effect of alternate moistening and drying varied with the different species. In a few instances the effect of drying on the percentage of germination was negligible. Germination in some species was hastened and the percentage of germination increased by alternate moistening and drying, while with others germination was delayed and the percentage of germination decreased. Rapid and slow drying varied in their effect on germination in a number of the species studied. The behavior of the seeds depends upon the particular species, the rate of drying, and the time when drying takes place.

In general, the seeds of the species which germinated at room temperatures may be placed in five groups: (1) seeds in which alternate moistening and drying had no effect on percentage of germination; (2) seeds in which the percentage of germination was increased under conditions of alternate moistening and drying; (3) seeds in which the percentage of germination was decreased under conditions of alternate moistening and drying; (4) seeds in which germination was increased with rapid drying and decreased with slow drying; and (5) seeds in which germination was decreased with rapid drying and increased with slow drying.

While alternate moistening and drying had no effect on percentage of germination of *Bromus polyanthus*, rapid drying slightly delayed and slow drying hastened its germination (fig. 1).

Seeds giving increased germination have been noted in table III. The amount of increase usually varied with rapid drying and slow drying. However, both types of drying gave the same increase in percentage of germination in *Stipa lettermani*. The most pronounced effect of increase in germination was found in *Lepidium* (fig. 6) and *Rumex*, with rapid drying, and in *Artemisia* and *Rudbeckia* with slow

drying. The highest percentage of germination obtained in *Androsace* was with seeds which had been subjected to alternating moisture conditions with rapid drying.

With some seeds germination continued during the period of drying. In test *B* the seeds of *Poa interior* (fig. 2) began to germinate before the petri dishes were opened to dry, and continued to germinate during the period of drying. The seeds thus subjected to drying gave a slightly higher percentage of germination in a shorter period of time than the seeds which had continuous moisture. The behavior of the two lots of *Poa secunda* seeds was similar to, but lower in percentage, than *P. interior*. Germination also continued during the slow drying of the seeds of *Bromus anomalus*, *B. polyanthus*, *Artemisia*, and *Rudbeckia* (fig. 9).

In several species the percentage of germination secured with continuous moisture was lower at the temperatures used than the maximum germination obtained under other conditions (table I). Although temperature conditions were not favorable, percentages of germination approaching the maximum were obtained in *Achillea* and *Lepidium* under alternating moisture conditions with rapid drying, and in *Artemisia*, *Plantago*, and *Rudbeckia* with slow drying. In these species the effect of temperature was overcome by drying. In *Stipa lettermani* and *Rumex mexicanus* the effect of temperature was overcome by drying only in part. Under conditions of alternating temperatures *Rumex* seeds gave 100 per cent germination in 12 days. The effect of drying on *Rumex* was slowly to bring about the changes in the seed which were quickly induced by alternating temperatures. The foregoing results suggest that the effect of drying in these seeds is associated, at least in part, with the problem of oxygen supply, as CROCKER (3) found for *Xanthium*.

Drying decreased the percentage of germination in the seeds of several species. The amount of injury varied with the species and was influenced by the time and rate of drying. *Pseudocymopterus* (fig. 8) illustrates this effect. Slow drying of *Geranium* decreased germination slightly by hardening the seed coat of the few seeds which did not germinate quickly. Rapid alternations of moistening and drying only retarded the process of germination. The behavior

of *Geranium* agrees with the conclusions of DUVEL, who found that the retardation in germination after dry storage was caused by changes in the seed coat.

The knowledge regarding the nature of the changes taking place in the seeds of each particular species is far from complete. Drying may have produced changes in the seed coat or embryo, or in both seed coat and embryo. JOSEPH (19) observed that drying parsnip seeds during the storage period affected the embryo and not the seed coat. KIDD and WEST (21) concluded that the redrying of *Brassica alba* seeds overcame secondary dormancy, but DAVIS (8) could not secure any benefit from redrying *Ambrosia trifida* seeds in which secondary dormancy had been induced. JONES (18) observed that desiccation of after-ripened *Acer saccharum* seeds reduced seedling vigor, and that if desiccation continued the embryos failed to germinate. FLEMION (12) found that drying partially or entirely after-ripened seeds of *Sorbus aucuparia* developed a secondary dormancy which required longer to overcome than the original period of dormancy. She discovered too, that while the chief cause of dormancy was in the embryo, the seed coat also contributed to delay after the embryo had after-ripened. The effect of drying therefore differs with the different types of seeds.

IMPORTANCE OF TIME AT WHICH DRYING OCCURS

The time at which drying occurs is very important with some seeds. The time of drying in relation to the stage of development of the germinating seed was probably a factor in producing the results shown in table III, where rapid and slow drying gave opposite results. The effect of decreasing resistance to drying is seen in the slow drying of *Poa interior*, *P. secunda*, *Achillea* (fig. 4), and *Androsace* (fig. 5), and in both types of drying of *Chrysanthamnus* and *Pseudocymopterus*. With rapid drying, which began late, *Bromus anomalus*, *Lupinus*, and *Rudbeckia* were injured. *Poa secunda* seeds with low viability did not withstand drying that started early in the germinative process. PFEFFER (27) calls attention to the fact that while resistant seeds can withstand drying and remoistening, seedlings are killed by drying, and resistance to drying decreases during germination.

Hastening of germination occurred in some seeds after slow drying (fig. 7) and in others after rapid drying (figs. 4, 8). In *Pseudocymopterus*, germination was hastened after the second period of rapid drying, although further drying decreased the percentage of germination. Such hastening and acceleration in germination of *Brassica alba* seeds after drying, as found by KIDD (20) and KIDD and WEST (21), may be due to the stage of development attained by the embryo while in a moist condition previous to drying, rather than to the influence of drying.

INFLUENCE OF CONDITIONS PREVIOUS TO DRYING

The influence of conditions previous to drying may be seen in the germination of some of the seeds which were dried for 105 days (table V). The three sets of *Melica* seeds were subjected to identical conditions during and after the period of drying. After drying and remoistening, followed by cold temperatures of 0° to 4° C. for 84 days, the seeds gave 94, 84, and 92 per cent germination respectively. Those seeds which had been placed at 19° to 24° C. for 35 days had not made as much development previous to drying as had the seeds which had been subjected to -1.5° to -2.5° C. for a part of the moist period, or those which had a longer period of moisture at the warmer temperatures. Although the percentage of germination was low, *Collomia* and *Ribes inebrians* also show the influence of conditions previous to drying. Here, as in *Melica*, the seeds which had been held at low temperatures previous to drying gave higher percentages of germination than those which had been given warm temperatures. Such results indicate that drying during the period of after-ripening had little, if any, effect upon the germination of seeds of *Melica*, *Collomia*, and *Ribes inebrians*.

EFFECT OF ALTERNATE MOISTENING AND DRYING AS SHOWN BY LATER TEST FOR VIABILITY

The effect of alternate moistening and drying was not shown on some seeds until after the period of alternating moisture conditions, when the seeds were placed in other conditions for germination. No germination was obtained during the time *Hordeum nodosum* and *Collomia linearis* seeds were subjected to alternating moisture con-

ditions with rapid drying. Apparently they were not harmed by such conditions and derived some benefit. In the test for viability following the period of alternate moistening and drying (table IV), *Hordeum* seeds from test B gave 74 per cent germination. While this was below the maximum obtained (table I), it was 50 per cent more than that secured from seeds under similar germinating conditions which had not previously been subjected to alternate moistening and drying. *Hordeum* seeds from test C which were dried for 105 days gave 94 per cent germination with alternating temperatures. (The percentage here is based on the original number of seeds and not on the number of seeds dried.) *Collomia* seeds which had been subjected to alternate moistening and drying in test B later gave the maximum germination obtained, 62 per cent, in a shorter period of time than seeds which had not been so treated.

When placed in new conditions for germination after the period of alternate moistening and drying, *Agropyron* and *Polemonium* each gave 20 per cent and *Pentstemon subglaber* gave 12 per cent additional germination. A few species gave less than 10 per cent germination.

Some seeds require a longer period for germination than was supplied to them in the test for viability following the period of alternate moistening and drying.

The effect of alternate moistening and drying on hardcoated seeds may be seen in *Lupinus parvislorus* and *Vicia americana*. In tests A, B, and C, the seed coats of both species were kept intact. Rapid alternations of moistening and drying retarded and decreased the germination of *Lupinus* somewhat, but had little effect on *Vicia*. Seeds of *Vicia* which were given continuous moisture gave no germination and seeds which were subjected to alternating moisture conditions gave only 5 per cent germination with either rapid or slow drying. After the period of alternate moistening and drying, the coats of the *Vicia* seeds which had not germinated in test B were broken by filing and the seeds again supplied with moisture. With this treatment 30 per cent additional germination was obtained, thus giving 35 per cent total germination for this set of seeds (table IV). At the same time, seeds which had not been subjected to alternating moisture conditions but in which the coats were broken by filing, gave 40 per cent germination.

Failure of seeds to germinate when placed in other conditions after 51 to 53 days of alternating moisture conditions, therefore, may have been due to injury from previous drying; to secondary dormancy produced by the drying, temperature, or moisture conditions; to lack of suitable germinating conditions; or in a few instances to lack of viability. Some seeds were injured by the alternate moistening and drying and others withstood repeated drying with little or no injury. Some of the *Poa secunda* seeds were not viable. Seeds from the second area had much lower viability than seeds from the first area. *Polygonum* seeds which failed to germinate and some seeds of *Pentstemon rydbergii*, *Acer grandidentatum*, and *Sambucus microbotrys* were found to be undeveloped. A few seeds molded during the period of testing, but many which failed to germinate still appeared sound. Since these seeds did not germinate with continuous moisture at room temperatures (22° to 29° C.) within the time employed, other conditions will have to be used for them before the effect of alternating moisture conditions can be determined. The seeds of a number of the species contain rudimentary embryos or embryos which require a long period of after-ripening before germination occurs.

EFFECT OF LONG PERIOD OF DRYING ON GERMINATION BEHAVIOR

Seeds which were dried for 105 days after a period of moistening also varied in their responses to germinating conditions (table V). Some may not have had suitable temperatures for germination, or the period may not have been long enough. One or more samples of each of four species, *Melica*, *Pentstemon rydbergii*, *Vicia*, and *Ribes montigenum*, gave higher percentages of germination after the long period of drying than the maximum germination obtained from seeds which were not so dried. Dried seeds of *R. inebrians* gave next to the highest germination obtained for the species. The behavior of *Melica* and *R. inebrians* seeds has been discussed in connection with the influence of conditions previous to drying. Of the two samples of *Vicia* seeds which were dried, those in which the seed coat had been broken by filing before they were remoistened gave 100 per cent germination. Those with coats intact gave no germination until later; when the coats were broken by filing, they also gave 100 per

cent germination. The long period of drying had no harmful effect on these seeds. The behavior of *V. americana* corresponds to the findings of MUNERATI and ZAPPAROLI for *V. segetalis*.

Some of the dried *Pentstemon rydbergii* seeds which failed to germinate were undeveloped, but 19 per cent germinated when remoistened. This was equal to 16 per cent of the original lot from which the dried seeds were taken. Previous to drying, 14 per cent had germinated, thus giving a total of 30 per cent for this lot of seeds, which was the maximum obtained for *P. rydbergii*. Thus germination was increased by drying the ungerminated seeds.

Little or no injury was shown by seeds of *Hordeum* and *Polemonium*. *Hordeum* seeds which had not been dried gave 100 per cent germination, and seeds which had been dried gave 96 to 97 per cent germination when subjected to alternating temperatures. *Polemonium* seeds which had been dried for 105 days gave 26 per cent germination while the maximum obtained in other tests was only 30 per cent.

Decreased germination of *Rumex* and *Orthocarpus* may have been due to injury or to secondary dormancy produced by drying, or by conditions which prevailed during the previous moist period. With alternating temperatures, *Rumex* seeds which had not been dried gave 100 per cent germination, but the seeds which had been dried after the period of alternating moisture conditions with slow drying gave only 86 per cent germination. *Orthocarpus* seeds gave 28 per cent germination when subjected to 0° to 4° C. for 87 days, but seeds which had been dried gave no germination although subjected to a temperature of 0° to 3° C. for a period of 91 days.

Lower percentages of germination than the maximum obtained with seeds which were not dried were obtained from the dried seeds of *Agropyron*, *Androsace*, *Chenopodium*, *Collomia*, *Frasera*, and *Gilia*. Besides *Orthocarpus*, which has been discussed, no germination occurred in the dried seeds of five other species, *Delphinium*, *Erythronium*, *Moldavica*, *Viola*, and *Sambucus*. Only one or two of the dried seeds of each species germinated in *Castilleja*, *Sophia*, and *Symphoricarpos*. Since several of these seeds have rudimentary embryos or embryos which require after-ripening, failure to germinate may have

been due to lack of suitable conditions for germination, or to secondary dormancy caused by drying rather than to injury or lack of viability.

EFFECT OF DRYING ON GERMINATION

The effect of drying on germination behavior is determined by the effect of drying on the seed itself. Drying seeds after they have absorbed water may affect them in one or more of the following ways:

1. Lack of sufficient moisture may arrest the development or growth of the embryo which precedes germination, until sufficient moisture is again supplied. When this is supplied development and growth proceed without injury and germination is only delayed.

2. Drying of the embryo at a critical stage in its growth, for example, when it is well developed just previous to or during the early stages of germination, when cell division is rapidly taking place, may injure it beyond the point of recovery and thus prevent further growth and germination when moisture is again supplied, as noted by KIDD, KIDD and WEST, and PFEFFER. This results in decreased germination.

3. Drying may bring about changes in the seed coat, making it more permeable to water or oxygen, or it may lessen the mechanical resistance of the coat to the developing embryo as found by LUDWIG and CROCKER (3, 4, 6). Such changes hasten and increase germination while the reverse of these changes in the seed coat may produce secondary dormancy, and thus delay or prevent germination (9).

4. Drying may bring about changes in the embryo which lower the vitality of the seed, decreasing germination, as found in the parsnip by JOSEPH and in the sugar maple by JONES (18); or it may produce secondary dormancy which delays and decreases germination until dormancy is again overcome, as in *Sorbus aucuparia* (12). Drying may bring about other changes in the embryo which hasten the development and germination of dormant seeds when moisture is again supplied. The behavior of some of the seeds used in this investigation indicates that the effect of drying may be on the embryo rather than on the seed coat. Further study is needed to determine definitely which part of the seed is affected.

The rate at which drying occurs and the time of drying often

determine whether it is harmful, beneficial, or negligible in its effect on germination. The amount of benefit or injury by alternate moistening and drying is difficult to determine, in some cases, until more is known about the normal germination behavior of the seeds. They vary considerably in their ability to withstand drying. Conditions which inhibit or delay the germination of seeds of one species stimulate and increase germination in another, and have no effect upon a third. The factors which bring this about can be determined only by further study of the individual species.

Summary

1. The seeds used in this study comprise 9 grass, 26 weed, and 7 woody species of Utah range plants. Twenty-three of the 42 species studied gave little or no germination at temperatures of 22° to 29° C. Other conditions must be used for them before the effect of alternate moistening and drying can satisfactorily be determined.

2. The effect of alternate moistening and drying on the germination of seeds varies with the individual species. Of the 19 species which germinated at 22° to 29° C., alternate moistening and drying had little effect upon the germination of *Bromus polyanthus*. It increased the germination of *Stipa lettermani*, *Artemisia incompta*, *Lepidium densiflorum*, and *Plantago breedyi*. It decreased the germination of *Geranium viscosissimum*, *Pseudocymopterus montanus*, *Chrysothamnus lanceolatus*, and *Stipa columbiana* (slightly).

3. Rapid drying had little effect upon the germination of *Poa interior*, *P. secunda*, and *Chenopodium album*, but increased the germination of *Achillea lanulosa*, *Androsace diffusa*, *Pentstemon rydbergii*, and *Rumex mexicanus*; in all of these species slow drying decreased the percentage of germination. Rapid drying decreased the germination of *Bromus anomalus*, *Lupinus parviflorus*, and *Rudbeckia occidentalis*, while slow drying increased the germination of *Rudbeckia* but had little effect upon *Bromus anomalus* and *Lupinus*.

4. Increased germination was usually accompanied by a hastening of the germinative process and decreased germination was accompanied by a retardation. In five species, however, *Poa secunda* no. 1, *Androsace*, *Plantago*, *Rudbeckia*, and *Rumex*, retardation was followed by increased germination.

5. Some seeds after they have absorbed water will withstand short periods of alternate drying and moistening, and some will withstand a long period of drying without injury. The time at which drying begins in relation to the stage of development of the germinating seed is a very important factor in determining whether drying is harmful or beneficial. The effect of drying is also influenced by the rate at which drying takes place.

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GREAT BASIN BRANCH STATION
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LITERATURE CITED

1. ATTERBERG, A., Die Nachreife des Getreides. Landw. Versuchs-Stat. **67**: 129-143. 1907.
2. ATWOOD, W. MCK., A physiological study of the germination of *Avena fatua*. BOT. GAZ. **57**:386-414. 1914.
3. CROCKER, WM., Rôle of seed coats in delayed germination. BOT. GAZ. **42**:265-291. 1906.
4. ———, Germination of seeds of water plants. BOT. GAZ. **44**:375-380. 1907.
5. ———, Longevity of seeds. BOT. GAZ. **47**:69-72. 1909.
6. ———, Mechanics of dormancy in seeds. Amer. Jour. Bot. **3**:99-120. 1916.
7. ———, and DAVIS, W. E., Delayed germination in seeds of *Alisma plantago*. BOT. GAZ. **58**:285-321. 1914.
8. DAVIS, W. E., Primary dormancy, after-ripening, and the development of secondary dormancy in embryos of *Ambrosia trifida*. Amer. Jour. Bot. **17**:58-76. 1930.
9. DUVEL, J. W. T., The vitality and germination of seeds. U.S. Dept. Agr. Bur. Pl. Ind. Bull. **58**. 1904.
10. EWART, A. J., Additional observations on the vitality and germination of seeds. Proc. and Trans. Liverpool Biol. Soc. **10**:185-193. 1896.
11. ———, On the longevity of seeds. Reprint Proc. Roy. Soc. Victoria. N.S. **21**. 1908.
12. FLEMION, FLORENCE, After-ripening, germination, and vitality of seeds of *Sorbus aucuparia* L. Contr. Boyce Thompson Inst. **3**:413-440. 1931.

13. GUPPY, H. B., Studies in seeds and fruits. Williams and Norgate, London. 1912.
14. HARRINGTON, G. T., and CROCKER, WM., Resistance of seeds to desiccation. Jour. Agr. Res. 14:525-532. 1918.
15. HÄNLEIN, H., Ueber die Keimkraft von Unkrautsamen. Landw. Versuchs-Stat. 25:465-470. 1880.
16. HILTNER, (see CROCKER, 6).
17. HITCHCOCK, A. S., Manual of the grasses of the United States. United States Dept. Agr. Misc. Publ. 200. 1935.
18. JONES, H. A., Physiological study of maple seeds. BOT. GAZ. 69:127-152. 1920.
19. JOSEPH, HILDA C., Germination and keeping quality of parsnip seeds under various conditions. BOT. GAZ. 87:195-210. 1929.
20. KIDD, F., The controlling influence of carbon dioxide in the maturation, dormancy and germination of seeds. Proc. Roy. Soc. (London) B. 87:408-421, 609-625. 1914.
21. ———, and WEST, C., The controlling influence of carbon dioxide. IV. On the production of secondary dormancy in seeds of *Brassica alba*, following treatment with carbon dioxide, and the relation of this phenomenon to the question of stimuli in growth processes. Ann. Bot. 31:457-487. 1917.
22. KIESSLING, L., Untersuchungen über die Keimung der Getreide. Landw. Jahrb. (Bayern) 1:449-514. 1911.
23. LUDWIG, F., Ueber durch Austrocknen bedingte Keimfähigkeit der Samen einiger Wasserpflanzen. (Ref. MULLER's work.) Biol. Centralbl. 6:299-300. 1886.
24. MUNERATI, O., and ZAPPAROLI, T. V., L'influenza dell' alternanzá dell' umidità e della siccità sulla germinazione dei semi delle erbe infestanti. Malpighia 24:313-328. 1912.
25. NOBBE, F., Über künstliche Getreide-trocknung mit Bezug. auf die Keimfähigkeit. Mitt. Deut. Landw. Gesell. 12:185-186. 1897.
26. ———, and HÄNLEIN, H., Ueber die Resistenz von Samen gegen die äusseren Factoren der Keimung. Landw. Versuchs-Stat. 20:71-96. 1877.
27. PFEFFER, W. F. P., Physiology of plants. (Trans. and edited by EWART, A. J.) 2:207-211; 252-254. Clarendon Press, Oxford. 1903.
28. PICKHOLZ, L., Ein Beitrag zur Frage über die Wirkung des Lichtes und der intermittierenden Temperatur auf die Keimung von Samen, sowie über die Rolle des Wassergehaltes der Samen bei dieser Wirkung. Zeitschr. Landw. Versuchsw. Oesterr. 14:124-151. 1911.
29. SAMPSON, A. W., Natural revegetation of range lands based upon growth requirements and life history of the vegetation. Jour. Agr. Res. 3:93-148. 1914.
30. ———, Important range plants: their life history and forage value. U.S. Dept. Agr. Bull. 545. 1917.

31. ———, Plant succession in relation to range management. U.S. Dept. Agr. Bull. 791. 1919.
32. ———, Native American forage plants. John Wiley and Sons, New York. 1924.
33. SCHRÖDER, G., Über die Austrocknungsfähigkeit der Pflanzen. Untersuch. Bot. Inst. Tübingen 2:1-52. 1886.
34. SHULL, C. A., The oxygen minimum and the germination of *Xanthium* seeds. BOT. GAZ. 52:453-477. 1911.
35. WAGGONER, H. D., The viability of radish seeds (*Raphanus sativus* L.) as affected by high temperatures and water content. Amer. Jour. Bot. 4:299-313. 1917.
36. ZADE, A., Der Flughafer. Inaug. Diss. Jena. 1-48. 1909.

